

Drag, Drafting, and Mechanical Interactions in Canopies of the Red Alga *Chondrus crispus*

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Abstract. Dense algal canopies, which are common in the lower intertidal and shallow subtidal along rocky coastlines, can alter flow-induced forces in their vicinity. Alteration of flow-induced forces on algal thalli may ameliorate risk of dislodgement and will affect important physiological processes, such as rates of photosynthesis. This study found that the force experienced by a thallus of the red alga *Chondrus crispus* (Stackhouse) at a given flow speed within a flow tank depended upon (1) the density of the canopy surrounding the thallus, (2) the position of the thallus within the canopy, and (3) the length of the stipe of the thallus relative to the height of the canopy. At all flow speeds, a solitary thallus experienced higher forces than a thallus with neighbors. A greater than 65% reduction in force occurred when the thallus drafted in the region of slower velocities that occurs in the wake region of even a single upstream neighbor, similar to the way racing bicyclists draft one behind the other. Mechanical interactions between thalli were important to forces experienced within canopies. A thallus on the upstream edge of a canopy experienced 6% less force than it did when solitary, because the canopy physically supported it. A thallus in the middle of a canopy experienced up to 83% less force than a solitary thallus, and forces decreased with increasing canopy density. Thus, a bushy morphology that increases drag on a solitary thallus may function to decrease forces experienced by that thallus when it is surrounded by a canopy, because that morphology increases physical support provided by neighbors.

Introduction

Algal canopies dominate space in the intertidal and shallow subtidal along rocky coastlines and provide secondary habitat for encrusting organisms as diverse as bryozoans,

hydroids, sponges, and tunicates. Algal canopies alter flow in their vicinity (Koehl and Alberte, 1988; Eckman *et al.*, 1989) in ways that determine such important phenomena as algal production and physiology (Taylor and Hay, 1984; reviewed by Hurd, 2000), the recruitment of algal propagules (Johnson and Brawley, 1998) and invertebrate larvae (Duggins *et al.*, 1990), the flux of gases and nutrients to the surface of algal thalli (Koehl and Alberte, 1988), and the potential for breakage of thalli due to flow-induced forces (Koehl and Wainwright, 1977; Dudgeon and Johnson, 1992; Gaylord *et al.*, 1994; Johnson and Koehl, 1994; Blanchette, 1997; Koehl, 1999; Gaylord, 2000).

Flow forces may limit the size of some algae (Carrington, 1990; Gaylord *et al.*, 1994; Denny, 1999; Gaylord, 2000), either by dislodgment of entire thalli or by pruning (Blanchette, 1997; Dudgeon *et al.*, 1999). However, most measurements of flow-induced forces on algal thalli have examined thalli only in isolation from their canopy (Charters *et al.*, 1969; Gerard, 1987; Koehl and Alberte, 1988; Sheath and Hambrook, 1988; Armstrong, 1989; Dudgeon and Johnson, 1992; Johnson and Koehl, 1994; Gaylord *et al.*, 1994; Shaughnessy *et al.*, 1996; but see Carrington, 1990; Holbrook *et al.*, 1991). A surrounding canopy, however, is likely to mediate flow-induced forces experienced by constituent thalli. For example, a canopy probably slows flow within (Koehl and Alberte, 1988; Eckman *et al.*, 1989), thus decreasing forces experienced by constituent algal thalli. Total force on an individual thallus, however, will be due both to direct fluid dynamic forces, such as drag, and to forces resulting from mechanical interactions with neighboring thalli (Holbrook *et al.*, 1991). This paper quantifies the dynamics of the interactions among adjacent thalli due to flow forces on individual thalli and on a canopy of the red alga *Chondrus crispus*.

C. crispus occurs in dense canopies (up to 4 stipes per cm²; S. Dudgeon, unpubl. data) on intertidal and shallow

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subtidal rocky shores along the northeast coast of the United States and Canada. In the Gulf of Maine, *C. crispus* can be found from about 1 m above mean low water to about 15 m below mean low water (Mathieson and Burns, 1971; Dudgeon *et al.*, 1999). It occurs in distributions that range from intermittent patches of thalli arising from a single holdfast to areas where the substratum is covered with a dense, uniform canopy (as tall as ~ 0.07 m in height when emersed at low tide; S. Dudgeon, California State University at Northridge, unpubl. data). A large specimen of *C. crispus* generally consists of a relatively long, narrow stipe topped by a bushy, bifurcated thallus (Fig. 1). Multiple stipes arise

from a persistent encrusting holdfast; thalli seldom occur in isolation from neighboring thalli.

Flow-induced dislodgment of subtidal *C. crispus* thalli has not been quantified. However, winter dislodgment of thalli from tall intertidal canopies (>4 cm tall) can be as great as 30% (Dudgeon and Johnson, 1992); and the seasonal decrease in biomass of the largest thalli in an intertidal population (which ranged in size from 2.5 cm² to 250 cm² in planform area) can be as great as 75% (M. Pratt and A. Johnson, unpubl. data). Because thalli regenerate quickly from persistent encrusting holdfasts, dislodgment is not typically a selective death for the genet. New thalli of *C.*

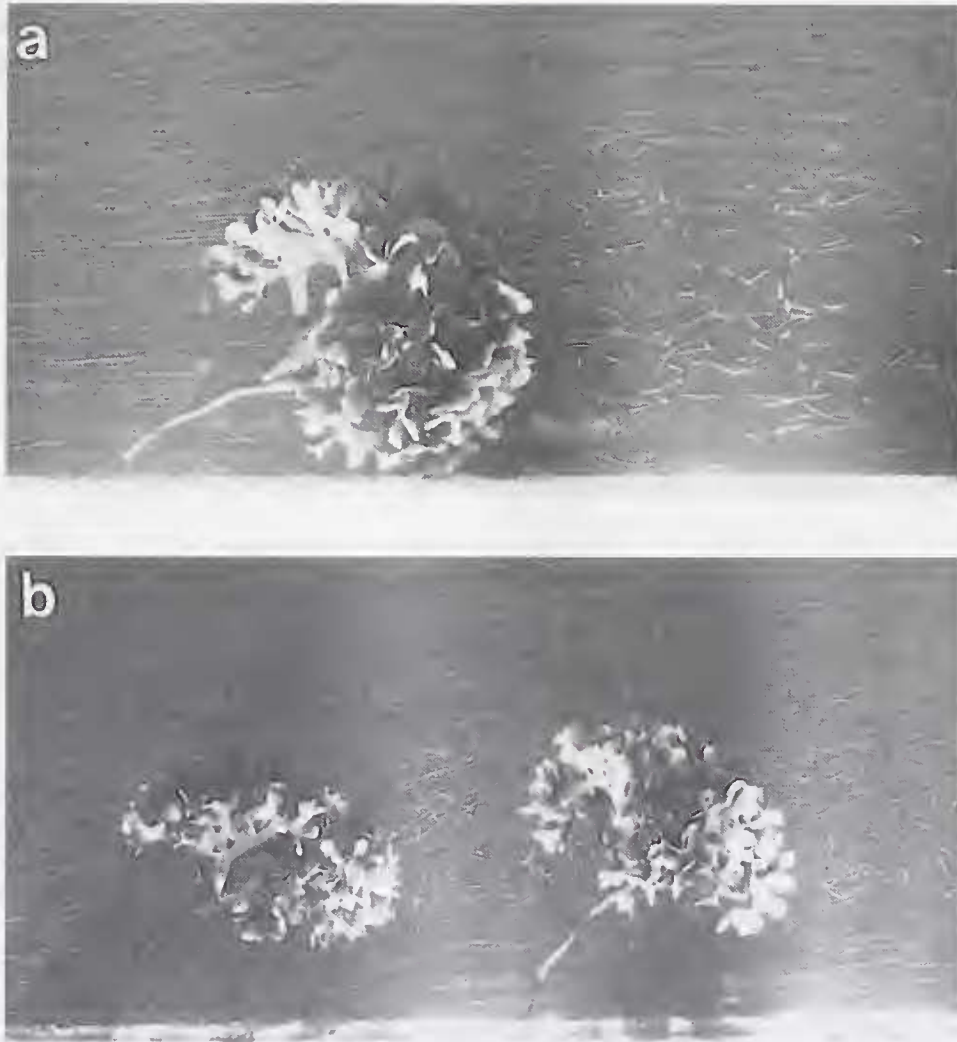


Figure 1. Long-exposure photographs of *Chondrus crispus* taken at an ambient flow speed of 0.10 m s⁻¹ showing (a) a solitary thallus and (b) a pair of thalli, where the thallus shown in (a) is in the downstream position. Flow direction is from left to right. For scale, the distance between stipes was 0.09 m. Only the middle section of the tank is illuminated by a narrow slit of light. Longer streaks indicate faster components of velocities in the downstream direction. Streaks at the top of the photograph are uniform in length, indicating freestream flow. Flow was slowed in the wake of thalli; drag was consequently less on the thallus shown in (a) when it drafted (b) within the wake of an upstream thallus. The lower drag is reflected by the decrease in bend of the stipe in (b) relative to (a).

crispus grow rapidly, outcompeting other species in the lower rocky intertidal of New England (Lubchenco, 1980; Dudgeon and Johnson, 1992; Dudgeon *et al.*, 1999).

In this study I examine how flow-induced forces on algal thalli depend on both the individual morphology of the thalli and on the density and morphology of the surrounding canopy. I specifically determine how flow-induced forces experienced by a thallus are influenced by (1) the density of the canopy, (2) the position of the thallus within the canopy, and (3) the length of stipe of a thallus relative to the height of the canopy.

Materials and Methods

Collection and maintenance of algae

Thalli of *Chondrus crispus* were collected at a shallow subtidal site at 9 m in depth located 0.2 km northeast of Canoe Beach, East Point, Nahant, Massachusetts (42° 25'N: 70° 54'W). Horizontal surfaces in the collection area, which was protected from extreme wave action, were dominated by *C. crispus*. Individual thalli, still attached to the holdfast at the base of the stipe, were maintained within circulating seawater tables at 15°C and were used in experiments within 2 weeks after their removal. Thalli remained healthy for the duration of experiments.

Quantification of flow and force

The downstream forces exerted by the stipe of a thallus on the substratum were measured by attaching the end of the stipe that was originally attached to the holdfast onto a force beam. That beam protruded downward through a hole in a flat, horizontally oriented, clear acrylic plastic plate located 0.2 m above the floor of a recirculating seawater flow tank (two flow tanks were used, each 0.2 m wide by 2 m long, similar to that described in Vogel and LaBarbera, 1978). There was freestream flow adjacent to the fronds of the canopy, as is evident in Figure 1, thus indicating that boundary effects from the bottom of the flow tank were negligible. Forces measured represented those due to drag but not due to acceleration; this is reasonable, as Gaylord (2000) found that forces due to acceleration contribute negligibly to wave-induced forces measured on algal thalli.

Experimental flow speeds were constrained by the maximum flow speeds attainable within each flow tank (0.21 m s⁻¹ in the flow tank used for the quantification of the C_D and E of solitary thalli; 0.45 m s⁻¹ in the flow tank used for canopy experiments), but were similar to monthly maxima measured over the period of a year at the collection site by an Interocean S4 recording electromagnetic flow meter. The mean flow speed each month was between 0.023 and 0.042 m s⁻¹, and the maximum flow speed each month was between 0.28 and 0.61 m s⁻¹ measured at 0.5 m off the substratum (K. Sebens, University of Maryland, unpubl.

data). Thalli used in these experiments were from this subtidal habitat. Maximum flow speeds experienced by intertidal specimens of *C. crispus* in breaking waves will be faster.

Experimental flow speeds (U) were calculated from the measured drag on a flat, circular disk (diameter = 3.62×10^{-2} m) oriented perpendicular to flow, using the standard empirical drag equation

$$D = \frac{1}{2} \rho U^2 C_D S \quad (1)$$

where D = drag, ρ = fluid density, U = flow speed, C_D = coefficient of drag, and S = projected area of the disk. The disk was attached to a force beam that projected 0.05 m below the water surface in the working section of the tank. The drag on the beam alone was subtracted from each measurement. Disks have a constant coefficient of drag, $C_D = 1.17$, over the range of Reynolds numbers used in this study (Hoerner, 1965); therefore the standard empirical drag equation (Eqn. 1) applies (Vogel, 1994).

In all treatments described below, total force on a thallus was quantified as the force that the thallus exerted on the force beam. Drag accounts for the total force acting on an individual thallus only when that thallus is not mechanically interacting with other thalli within the canopy. Therefore, I call the force exerted on the beam "drag" when there were no mechanical interactions between thalli, and "total force" when there were also mechanical interactions between thalli.

Coefficient of drag

Drag measurements (at $U = 0.21$ m s⁻¹) were used to calculate the coefficient of drag (C_D) for eight solitary thalli using Eqn. 1, where S = planform area of the thallus. The planform area of each thallus was measured to the nearest 0.01 cm² by digitizing the outlines of a photograph of a thallus that had been pressed flat between two plates of glass, such that the branches of each thallus did not overlap. This measurement of planform area is equivalent to the "planform area" (Carrington, 1990), the "actual planform area" (Johnson and Koehl, 1994), the "maximal projected blade area" (Gaylord *et al.*, 1994), the "total projected blade area" (Gaylord and Denny, 1997), the "maximum projected blade area" (Denny *et al.*, 1997), and the "real area" (Koehl, 2000) quantified by other researchers. For *C. crispus*, which has a complex three-dimensional morphology, this measurement of planform area represents the most reliable and repeatable measure of S . The change in frontal area that occurs as a function of flow speed is accounted for by changes in the C_D . The eight solitary thalli used for these measurements ranged in mass from 2.6 to 7.2 g (mean = 4.5 g, SE = 0.6) and in planform area from 0.0031 to 0.0092 m² (mean = 0.0061 m², SE = 0.0008).

Reconfiguration in flow

Flexible structures such as algae reconfigure in flow as velocity increases such that their relative drag is reduced at higher flow speeds. For solitary thalli, a useful measure of velocity-dependent relative drag reduction is the E -value (Vogel, 1984), which quantifies this relative reduction in drag (*i.e.*, the decrease in C_D with increase in velocity),

$$\frac{D}{U^2} = K_E U^E \quad (2)$$

where D = drag at a particular flow speed (U). A value for E is determined as the slope of a linear regression of $\log(D/U^2)$ versus $\log U$ for regions of this graph without inflection points; K_E is the antilog of the intercept of this line. The magnitude of E is zero for a structure, such as a rigid sphere, that does not reconfigure in flow. The steeper the negative slope (*i.e.*, the greater the absolute value of the negative slope), the greater the relative drag reduction experienced with an increase in velocity as a consequence of reconfiguration.

E and K_E were determined for the same eight solitary thalli of *C. crispus* for which the C_D was quantified (described above).

Canopy experiments

For all treatments in the canopy experiments, force exerted by one thallus (mass = 7.9 g, planform area = 0.01 m²) on the force beam was determined at flow speeds of 0.09, 0.18, 0.27, 0.36, and 0.45 m s⁻¹. All measurements were repeated three times (sufficient sampling given the low variance observed). All statistical comparisons between treatments, using ANOVA, are for force determined at the

highest experimental flow speed (0.45 m s⁻¹). Scheffé F -tests were used for *a posteriori* comparisons between treatments.

At all experimental velocities and for all treatments, forces on the stipe of the experimental thallus were quantified when it was 0.05 m long (*i.e.*, only half the length of the stipe protruded into flow, which was the same as the length of the stipes of the rest of the canopy), and 0.10 m long (*i.e.*, the full length of the stipe protruded into flow, which was twice the length of the stipes of the rest of the canopy). Forces on the experimental thallus were quantified for the following treatments: (1) in isolation (Fig. 1a); (2) in the presence of one other thallus (of approximately the same size and shape as the experimental thallus) located 0.09 m upstream (Fig. 1b); (3) on the upstream edge, middle, and downstream edge of a lower density canopy (0.08 thalli per cm²; Fig. 2); and (4) in the middle of a higher density canopy (0.16 thalli per cm²).

The lower density experimental canopy, which consisted of 32 thalli, mimicked the observed maximum density of the bushy tops of *C. crispus* in a typical shallow subtidal zone where they were collected (0.08 thalli per cm²; determined by counting the bushy tops within 20, 100 cm² quadrats). For experimental simplicity, the higher density experimental canopy, which consisted of 64 thalli, was chosen to double that of the lower density experimental canopy. That density is similar to that of large thalli (those with more than five branches) that occurred in a low intertidal habitat (number of 5 × 5 cm quadrats = 5; mean density = 0.2 thallus per cm², SE = 0.07; S. Dudgeon, unpubl. data).

Canopies were created by fastening individual thalli to a flat plate and suspending the plate upside down in the flow tank. Canopy thalli were positioned into regularly spaced,



Figure 2. Sketch from a long-exposure photograph of a low-density canopy of *Chondrus crispus* (0.08 thalli per cm²) at an ambient flow speed of 0.1 m s⁻¹. Flow direction is from left to right. For scale, the distance from the stipe at the leading edge to the stipe on the trailing edge was 0.2 m. Streaks between the thalli of the canopy were shorter, indicating that flow was slowed within the canopy. Forces were less on thalli associated with a canopy not only because flow was slowed (*i.e.*, drag was reduced), but also because the canopy provides mechanical support: thalli were most bent over at the upstream edge of the canopy but were more erect than the more isolated thalli shown in Figure 1.

staggered arrays by inserting the narrow end of the stipe through 1-mm holes in the plate and holding the stipes in place by means of soft modeling clay. Every other row of thalli was offset from the one before it so that any given thallus within the canopy was directly downstream of another thallus two rows in front of it. The length of the stipes of the thalli within the canopy was always 0.05 m from the surface of the plate.

Results

Thalli reorient in flow

When exposed to flow, a solitary thallus of *Chondrus crispus* immediately flopped over close to the substratum with the stipe reoriented parallel to flow (Fig. 1a). A thallus also reoriented when downstream of a single other thallus but bent over less than when solitary at the same ambient flow speed (Fig. 1b). In contrast, thalli within the canopies bent over less than did solitary thalli (Fig. 2).

Coefficient of drag and E of solitary thalli

The C_D of eight solitary thalli (measured at 0.21 m s^{-1} ; range = 0.46 to 0.83, mean = 0.60, SE = 0.046) was independent of thallus size; linear regression analysis: (1) C_D by mass (g): $F_{(1,7)} = 1.8$, $P = 0.22$, (2) C_D by planform area (m^2): $F_{(1,7)} = 2.6$, $P = 0.18$.

The E of those eight thalli (range = -0.46 to -0.92 , mean = -0.64 , SE = 0.06) was independent of thallus size (linear regression analysis: $F_{(1,7)} = 2.1$, $P = 0.19$ [E by thallus mass]; $F_{(1,7)} = 1.2$, $P = 0.31$ [E by thallus area]). The magnitude of K_E increased with increasing thallus mass (linear regression analysis: $F_{(1,7)} = 6.8$, $P = 0.04$, $r^2 = 0.53$):

$$K_E = 0.132 M^{1.04}, \quad (3)$$

where the units for the coefficient were $\text{kg}^{-0.04} \text{ m}^{-0.36} \text{ s}^{-0.64}$. By substituting the values for E and K_E into Eqn. 2, it can be seen that drag for these thalli can be modeled as:

$$D = 0.132 M^{1.04} U^{1.36} \quad (4)$$

Drafting behind upstream thalli

The drag on the solitary experimental thallus of *C. crispus* used in the canopy experiments was 0.16 N (SE = 0.0015 N; measured at a flow speed of 0.45 m s^{-1} ; Fig. 3). Doubling the length of the stipe on this thallus increased drag by only 6% (mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.16 N (short); 0.17 N (SE = 0.00017 N, long); $t_{(4)} = 3.2$, $P = 0.03$). The $C_{D@0.45 \text{ m s}^{-1}}$ of the thallus used in the canopy experiments was 0.16.

At 0.45 m s^{-1} , drag on the experimental thallus decreased by more than 65% (ANOVA: $F_{(2,8)} = 2360$, $P \ll 0.0001$; Fig. 3) whether it was downstream of only a single thallus

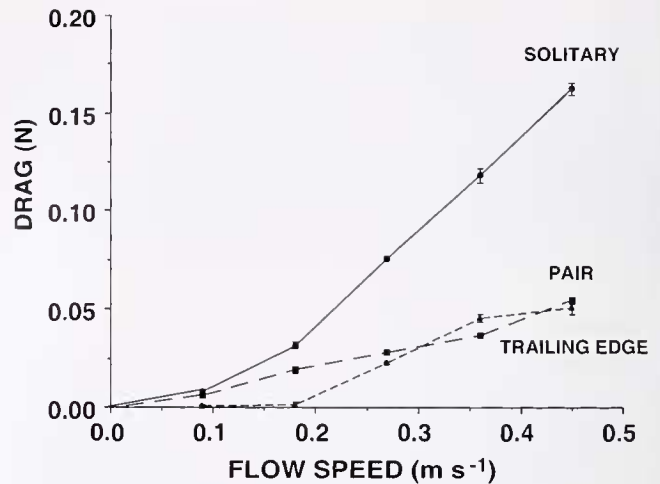


Figure 3. Drag (N) as a function of flow speed (m s^{-1}) for an experimental thallus of *Chondrus crispus* when solitary (circles, solid line), 0.09 m downstream of a single other thallus (squares, long dashed line) and on the trailing edge of a low-density canopy (triangles, short dashed line). Bars represent two standard errors about the mean; where not visible, these bars were smaller than the symbols.

(mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.055 N, SE = 0.00087 N) or of an entire canopy of thalli (mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.051 N, SE = 0.0014 N). Drag on the thallus at this flow speed was independent of whether there was only a single thallus or an entire canopy of thalli upstream (Scheffé F -test). Doubling the length of the stipe on this thallus when it was located on the downstream edge of a canopy increased the drag it experienced by 19% (mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.051 N [short]; 0.063 N [SE = 0.0026 N, long]; $t_{(4)} = 4.3$, $P = 0.01$).

Mechanical interactions between thalli

Total force on the experimental thallus decreased when the thallus was placed in the middle of an algal canopy (ANOVA: $F_{(2,8)} = 561$, $P \ll 0.0001$; Fig. 4) and decreased more with increasing density of the canopy (Scheffé F -tests; mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.089 N [SE = 0.0046 N, low density]; 0.028 N [SE = 0.00054, high density]). Thus, there was an 83% decrease in total force for this thallus in the middle of a dense canopy. Surprisingly, total force on the thallus when surrounded by a low density of neighboring thalli was greater than when it drafted in the wake of a single upstream neighbor (Scheffé F -tests; compare Fig. 3 "Pair" with Fig. 4 "Low density"). Doubling the length of the stipe did not significantly alter the total force the thallus experienced in the mid-canopy position (mean force $_{(0.45 \text{ m s}^{-1})}$ = 0.089 N [short]; 0.079 N [SE = 0.0071 N, long]; $t_{(4)} = -1.2$, $P = 0.31$).

Forces on the experimental thallus varied with position in the canopy (ANOVA $_{(0.45 \text{ m s}^{-1})}$; $F_{(3,11)} = 244$, $P \ll 0.0001$; Fig. 5), decreasing with increasing distance down-

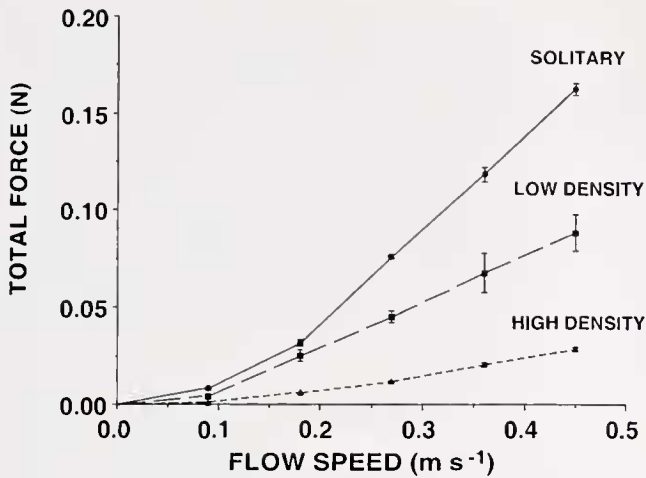


Figure 4. Force (N) as a function of flow speed (m s^{-1}) for an experimental thallus of *Chondrus crispus* when solitary (circles, solid line), in the middle of a low-density canopy (squares, long dashed line) and in the middle of a higher density canopy (triangles, short dashed line). Bars represent two standard errors about the mean; where not visible, these bars were smaller than the symbols.

stream of the upstream edge (Scheffé F -tests). When the experimental thallus was placed at the upstream edge of the low density canopy it experienced only 6% lower total force than when solitary (Scheffé F -test; mean force_(0.45 m s^{-1}) = 0.16 N [solitary]; 0.15 N [SE = 0.0042 N, upstream edge]; Fig. 5). Doubling the length of the stipe of this thallus in this upstream position increased the total force experienced by the thallus by 6% (mean force_(0.45 m s^{-1}) = 0.15 N [short]; 0.16 N [SE = 0.0028 N, long]; $t_{(4)} = 3.65$, $P = 0.02$).

Discussion

Understanding the consequences of flow to organisms entails not only examining their flow-related characteristics in isolation, but also, where appropriate, in the presence of surrounding neighbors. In marine environments, interactions among closely spaced neighbors can alter feeding currents around suspension-feeders such as sea anemones (Koehl, 1976), sabellid polychaetes (Merz, 1984), bryozoans (Okamura, 1988), and phoronids (Johnson, 1990, 1997), and can influence the productivity of algae (Taylor and Hay, 1984; Holbrook *et al.*, 1991; Dudgeon *et al.*, 1999) and seagrass (Koch, 1994). Effects on feeding and productivity occur, in part, because the presence of a canopy can alter turbulent mixing (reviewed in Worcester, 1995) and slow flow in seagrass (Fonseca *et al.*, 1982; Eckman, 1987; Gambi *et al.*, 1990; Worcester, 1995; Koch and Gust, 1999), kelp (Koehl and Alberte, 1988; Eckman *et al.*, 1989; Duggins *et al.*, 1990; Jackson, 1998), and intertidal macroalgae (this study, see Fig. 2). Alteration of flow within canopies also influences recruitment of planktonic larvae (Eckman,

1983, 1987; Jackson, 1986; Duggins *et al.*, 1990), algal propagules (Johnson and Brawley, 1998), and surfgrass seeds (Blanchette *et al.*, 1999). Canopies can also influence the subsequent growth of both invertebrates (Eckman, 1987; Eckman and Duggins, 1991) and plants (Holbrook *et al.*, 1991; Johnson and Brawley, 1998; Koch, 1999); and the risk of flow-induced dislodgment can be altered by living in dense conspecific populations as diverse as mussels (Harger and Landenberger, 1971; Bell and Gosline, 1997) and kelp (Koehl and Wainwright, 1977).

Experiments presented here show that flow-induced forces on thalli of the red alga *Chondrus crispus* must be considered in the context of interactions with neighboring thalli. The following discussion first examines how a solitary thallus of *C. crispus* orients in flow as velocity increases, and then goes on to examine the consequences of canopies to the reorientation of, and forces experienced by, a thallus.

Drag in isolation: How much do thalli reconfigure in flow?

Drag reduction is the most common mechanism considered when examining force reduction in flow. The E for solitary thalli of *C. crispus* (mean = -0.64) indicates that flexibility of the thalli resulted in a lower drag than the thalli would have experienced had they not reconfigured as velocity increased. Although this E is less negative (*i.e.*, represents a more shallow slope) than that of many other species of large macroalgae (*e.g.*, *Sargassum filipendula*: -1.06 to -1.47 , Pentcheff, value given in Vogel, 1984; *Hedophyllum sessile*: -0.57 to -1.2 , Armstrong, 1989; *Nereocystis luetkeana*: -0.75 to -1.2 , Johnson and Koehl,

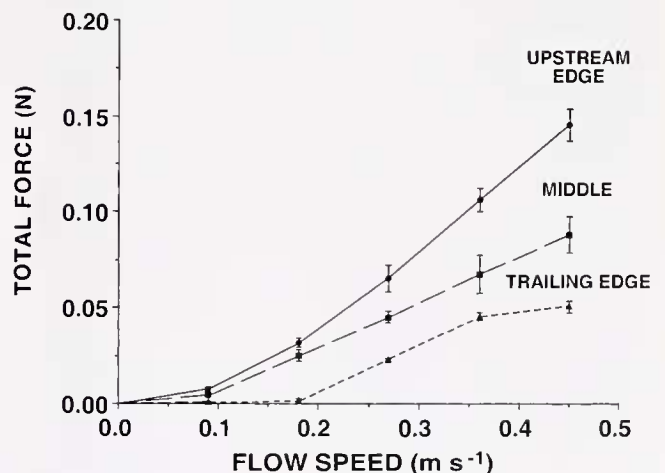


Figure 5. Force (N) as a function of flow speed (m s^{-1}) for an experimental thallus of *Chondrus crispus* when on the upstream edge (circles, solid line), middle (squares, long dashed line), and trailing edge (triangles, short dashed line) of a low-density canopy. Bars represent two standard errors about the mean; where not visible, these bars were smaller than the symbols.

1994), it is within the range of that determined for freshwater red algae (-0.33 to -1.27 ; Sheath and Hambrook, 1988), as well as for seven other species of intertidal macroalgae that are more similar in size to *C. crispus* (-0.28 to -0.76 , Carrington, 1990).

A small absolute value for a negative E can occur for thalli that are initially well-streamlined (low C_D over all flow speeds) such that additional rearrangement of the thallus has little effect on relative drag reduction with increasing flow speed (Armstrong, 1989; Johnson and Koehl, 1994). This is not the case for *C. crispus*: the coefficient of drag for *C. crispus* is relatively high at low flow speeds (this study: mean $C_D = 0.60$ at 0.21 m s^{-1} ; Dudgeon and Johnson, 1992: mean $C_D = 0.48$ at 0.21 m s^{-1} , $n = 33$) even for a small intertidal macroalga (Carrington, 1990). Thus, drag reduction, either by built-in streamlining (low C_D over all velocities, small absolute value of E) or by rearrangement into a more streamlined shape (high C_D at low velocities, but large absolute value of E), appears to be relatively unimportant to *C. crispus*. Perhaps drag reduction is a relatively unimportant source of force reduction when thalli are within a dense canopy of surrounding thalli.

Reduction of forces in canopies: The role of drafting and mechanical interactions between thalli

The response of the experimental thallus of *C. crispus* to flow differed dramatically between the solitary, paired, and within-canopy treatments. Differences in response were reflected in the degree to which thalli reoriented and by the magnitude of the forces experienced by the stipe in a given flow. The solitary experimental thallus, which experienced the greatest reorientation, also experienced the greatest forces; the presence of even a single upstream neighbor decreased the reorientation of, as well as the force on, that thallus. These changes occurred because the downstream (experimental) thallus was within the area of slowed water movement in the wake of the upstream thalli (Fig. 1b). I call this phenomenon "drafting" by analogy to the strategy racing bicyclists use, whereby a bicyclist rides in the wake of the bicycle in front. Thus, the higher drag on a downstream thallus with a longer stipe probably occurred because the longer stipe placed that thallus into a faster region of the wake of the upstream thallus.

Since flow speed within the canopy is expected to decrease with increasing canopy density (Gambi *et al.*, 1990), it is tempting to conclude that the decrease in force experienced by the thallus within a canopy was also due to a concomitant decrease in its drag. Just drafting in the wake of a single upstream neighbor, however, reduced force on the experimental thallus more than being surrounded by the lower density canopy. Why might the presence of a surrounding canopy result in a *higher* force than just a single neighbor?

The experimental thallus in the middle of a canopy could not collapse and reorient in the same way as a solitary thallus (compare Fig. 1 with Fig. 2). It was mechanically supported by the surrounding canopy, as well as being physically pushed and pulled by its surrounding neighbors. Thus, forces within algal canopies are due not only to hydrodynamic drag on specific individual thalli, but are also a result of physical interactions within the surrounding canopy. Upstream thalli were also mechanically supported by the canopy (Fig. 2), as seen by the reduced force on a thallus in this position when compared with that on the solitary thallus.

Similarly, Holbrook *et al.* (1991) found that dense stands of the sea palm *Postelsia palmaeformis* provided mechanical support for central members, which drooped over when the surrounding neighbors were removed. In contrast, Koehl and Wainwright (1977) suggested that mechanical entanglements between thalli of the giant kelp *Nereocystis luetkeana* increase loads on unbroken stipes in a tangled group of broken and unbroken thalli, thereby increasing the probability of breakage of the unbroken stipes within the canopy. A critical difference between these two species is that *P. palmaeformis* resists gravitational forces in air with short, wide stipes, whereas *N. luetkeana* resists hydrodynamic forces in pure tension by means of long, slender stipes. *C. crispus* is more similar to *N. luetkeana* in that the stipes resist hydrodynamic forces in tension, but is dissimilar in that downstream individuals of *C. crispus* can provide mechanical support to upstream thalli and in that the smaller size of *C. crispus* is likely to make any specific entanglements between thalli easier to untangle and less likely to promote dislodgement.

My results are in contrast to those of Carrington (1990), who found only minor drag reduction among groups of up to six thalli of *Mastocarpus papillatus*, a similar species of intertidal red alga (both species are in the order Gigartinales). There are several reasons for the differences in our results. Firstly, there were methodological differences between the studies. The canopies that I mimicked, which consisted of 32 and 64 thalli, were larger than that of Carrington (1990). The more extensive canopies used in my study better mimic those in which *C. crispus* naturally occurs. Furthermore, Carrington (1990) measured drag on the entire group of thalli (not on an individual thallus within the group) and then divided the total drag for that group by the sum of the drags measured for each individual thallus. While this method will give an estimate of drag reduction experienced by the entire group (*e.g.*, Vogel, 1989), it will fail to reveal much about forces experienced by individual thalli in different positions within the group. The latter is more important because it is the individual stipes of the thalli that typically break, not the holdfasts (which can be shared by multiple thalli).

Secondly, the differences between the results of our stud-

ies could be due to differences in the morphology of the species we studied. For example, unlike the majority of intertidal seaweeds, including *M. papillatus*, large *C. crispus* thalli do not lay flattened on the substratum when emersed during low tides but instead are supported by the three-dimensional branches of their thalli. Furthermore, comparisons of C_D between these studies indicate that *C. crispus* (this study: subtidal $C_{D(0.21 \text{ m s}^{-1})} = 0.46\text{--}0.83$; mean $C_{D(0.21 \text{ m s}^{-1})} = 0.60$; Dudgeon and Johnson [1992]: intertidal $C_{D(0.21 \text{ m s}^{-1})} = 0.19\text{--}1.1$, mean $C_{D(0.21 \text{ m s}^{-1})} = 0.48$, $n = 33$; M. Pratt and A. Johnson [unpubl. data]: intertidal $C_{D(0.55 \text{ m s}^{-1})} = 0.14\text{--}0.91$, mean $C_{D(0.55 \text{ m s}^{-1})} = 0.39$, $n = 149$) has an overall higher drag morphology than *M. papillatus* ($C_{D(1 \text{ m s}^{-1})} = 0.02\text{--}0.27$; predicted $C_{D(0.21 \text{ m s}^{-1})} = 0.28$; Carrington, 1990). These results suggest that intertidal *M. papillatus* is a more streamlined alga (relatively low C_D over all velocities) than *C. crispus* and would therefore be less subject to mechanical interlocking of thalli within a canopy.

A streamlined or streamlining morphology typically reduces the drag on macroalgae (Vogel, 1984; Johnson and Koehl, 1994; Koehl, 1986; Gerard, 1987; Koehl and Alberte, 1988; Armstrong, 1989). However, for smaller macroalgae that live in dense canopies, a morphology that enhances mechanical interactions between thalli (small absolute value for a negative E , high C_D) may be more important than a low-drag morphology to the mediation of forces ultimately experienced at the stipe. Furthermore, increases in density of the canopy cause decreases in the forces experienced, which may be important to dislodgment.

Thus, the density of a canopy of *C. crispus* as well as the bushiness and morphology of constituent thalli are important ecophysiological variables in the population dynamics of *C. crispus*. There is considerable morphological variation in *C. crispus* (Chopin and Floch, 1992), which is associated with differences in flow habitat and tidal height (*e.g.*, more dichotomies per unit length at less exposed, high intertidal sites; Gutierrez and Fernandez, 1992), and with differences in water temperature (*e.g.*, faster growth rates and more branches per unit length produced at higher temperatures; Kübler and Dudgeon, 1996). The increased photosynthetic area associated with greater branching is likely to increase productivity of those thalli (Kübler and Dudgeon, 1996). An increase in photosynthetic area, as well as decreased shading from neighbors (which might be associated with a more bushy morphology), could be particularly important to subtidal populations where light is often limiting. Increased size and more extensive branching will also increase the drag of individual thalli, but might, *via* mechanical interactions with adjacent thalli, increase the protection conferred by canopies.

Do canopies reduce risk of dislodgment?

For *C. crispus*, the presence of a canopy clearly decreases the forces on, and increases the upright orientation of, constituent thalli. If such forces were an important source of thallus loss, one might reasonably conclude that canopies reduce risk of dislodgment of thalli within the canopy. However, for *C. crispus* thalli growing subtidally, the drag determined on the solitary thallus in this study (0.16 N measured at 0.45 m s^{-1}) was more than an order of magnitude less than that required to break healthy, undamaged stipes of *C. crispus* (breaking force = 3 to 12 N; Dudgeon and Johnson, 1992). An order of magnitude difference persists even if the standard drag equation (Eqn. 1) is used to overestimate the force on a stipe at the highest flow speed measured in the field in the subtidal habitat where *C. crispus* was collected for this study (0.3 N; 0.61 m s^{-1}). This result indicates that subtidal thalli of *C. crispus* have an environmental stress factor (ESF; calculated as the ratio of breaking force to the force due to drag) of at least 10. ESF is a safety factor calculated over a specific time period (*e.g.*, a season) or a life-history stage rather than over a lifetime: *sensu* Johnson and Koehl, 1994. High values of ESF imply relative safety, whereas low values of ESF imply higher risk of dislodgement. Thus, only thalli otherwise compromised by damage are likely to break in this subtidal habitat (see Biedka *et al.*, 1987, and Denny *et al.*, 1989, for a discussion of the contribution of cracks to the fracture mechanics of macroalgae).

In contrast, the largest thalli of intertidal *C. crispus* from the summer populations are typically dislodged during fall and winter storms (Dudgeon and Johnson, 1992; M. Pratt and A. Johnson, unpubl. data). So, intertidal canopies do not prevent thallus dislodgment. They probably do, however, increase the flow speed at which a thallus of a given size can persist in the intertidal. An example calculation will illustrate this point. Although subtidal thalli can sometimes have longer stipes, larger size, and greater branching than do intertidal thalli (*pers. obs.*), thalli similar in size (m^2) and shape (C_D) to those used in the present experiments occur at intertidal sites; the experimental thalli used in the present study overlap in terms of both C_D (t -test, $P_{1,46} = 0.41$) and planform area (t -test, $P_{1,46} = 0.79$) with the largest thalli found in two dense intertidal canopies in Maine in the autumn (M. Pratt and A. Johnson, unpubl. data). Because of the similarity in size and shape of the subtidal and intertidal thalli from these two studies, the E -value from this study (Eqn. 4) can be used to estimate the drag of the intertidal thalli, and thereby their ESF, at the site-relevant maximum flow speeds for these intertidal sites in the autumn (M. Pratt and A. Johnson, unpubl. data). This method might still overestimate drag (underestimate ESF) if the E of intertidal thalli were more negative than those of the subtidal thalli (*i.e.*, the intertidal thalli were more flexible). Counterbal-

ancing this possibility is that this method of estimation (as used by Gaylord *et al.*, 1994; Denny, 1995; Bell, 1999) tends to underestimate drag (overestimate ESF) because E tends to get less negative at higher flow speeds as thalli reach their maximum ability to reconfigure (Bell, 1999). Even though this method tends to underestimate drag at higher flow speeds, 83% of the largest thalli found at these intertidal sites in the autumn are predicted to have a maximum drag greater than the maximum breaking force for their stipes. Thus, 83% of thalli have an $ESF < 1$ (mean $ESF = 0.62$ [SE = 0.06], t -test: $P_{(1,39)} < 0.001$) that the mean ESF is equal to 1; range $ESF = 0.1$ – 1.5).

The unexpected presence of these thalli in the autumn intertidal could result in part from differences in local flow microhabitat; however, this seems unlikely as the flow measurements were made in the middle of the algal canopy. Thalli might also persist if their C_D values at these high flow speeds were lower than those predicted from the E -value used; however, this is also unlikely as the method used already tends to give a low estimate for the C_D (Bell, 1999). Instead, thalli may persist at higher flows than predicted from estimates on individual thalli because of the mediation of those forces by the surrounding canopies.

Canopies matter

Measurements of drag, C_D , and E of isolated thalli must be considered in the context of the forces that thalli experience within canopies. This is because the morphology of thalli may influence breakage not only because of their individual drag characteristics, but also because of the way that morphology influences the forces that they experience within canopies. Even in the absence of breakage, canopy-induced changes in forces on thalli are important. The consequent reorientation and reconfiguration of thalli are likely to affect important processes, such as rates of photosynthesis (Greene and Gerard, 1990; Norton, 1991; Wing and Patterson, 1993; Kübler and Raven, 1994) or the probability of fertilization (Brawley and Johnson, 1992). For algae that live in canopies, an understanding of the consequences of the interaction of their morphology with flow requires information not just in isolation, but also within the canopies they compose.

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